Agricultural and Forest Meteorology 249 (2018) 57–70

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Maize leaf functional responses to drought episode and rewatering

He Song[a,b], Yibo Li[a,b], Li Zhou[c], Zhenzhu Xu[a,*], Guangsheng Zhou[a,c,*]

[a] State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China
[b] University of Chinese Academy of Sciences, Beijing 100049, China
[c] Chinese Academy of Meteorological Sciences, China Meteorological Administration, Beijing 100081, China

ARTICLE INFO

Keywords:
Climate change
Drought episode
Irrigation regimes
Leaf age
Photosynthetic potentials
Zea Mays L.

ABSTRACT

Effects of crop growth and physiological activities to drought and irrigation regimes have been extensively studied; however, the combined responses of plant growth, morphological and photosynthetic behaviors to drought episodes and thereafter rewatering receive a less attention. This field experiment was carried out directly *in situ* at an agricultural ecosystem research station across two entire growing seasons during 2015–2016, in northeastern China, on the renowned northeastern maize production belt, where is being threatened by severe drought. A field automatic rain-shelter was used, and five irrigation regimes including control, four drought episodes, and rewatering treatments were established. The chlorophyll contents (SPAD values), light-saturated photosynthetic rate (A_{sat}), and photosystem II actual quantum yield (Φ_{PSII}), maximum quantum yield (F_v'/F_m') decreased at lower leaf positions and with plant development. Episodic drought effects on plant growth, leaf morphological traits and photosynthetic processes at both vegetative and reproductive stages were severely remarked, particularly at late development stage and with longer drought duration. The recovery of leaf functional traits of the plants experienced historical-drought following re-irrigating was not fully restored to the level of the plants subjected to ample and normal water status; and the strength of recovery was proportional to the persistence of pre-drought episodes. The relationship of A_{sat} with SPAD depends on water status and plant development. A principal component analysis can well denote the change patterns in responses to water status treatments with plant development. The results may give an insight into how to understand the maize traits' responses to drought episode and rewatering, and this also might assist the drought-stricken crops to cope with future climatic change.

1. Introduction

Climate change results in abnormal changes in precipitation pattern in terms of both its total amounts and episodic drought frequencies (Alley et al., 2003; Trenberth et al., 2014; IPCC, 2014). Water shortage is a crucial constraint to crop growth, yield, physiological processes in many areas around world, including rain-fed and deficit-irrigation regions; meanwhile the abnormal occurrences of drought episodes usually fluctuate at various spatial-temporal scales (Boyer, 1982; Battisti and Naylor, 2009; IPCC, 2014; Rurinda et al., 2014; Myers et al., 2017). Intensifying drought also may reduce and even eliminate the expected benefits from some fewer favorite factors due to climate change such as elevated CO_2 and enhanced anthropogenic nitrogen (N) deposit (Iversen and Norby, 2014; Gray et al., 2016; Xu et al., 2016), and climatic warming may exacerbate drought disaster by further reducing soil moisture availability (Lobell et al., 2011, 2014; Iversen and Norby, 2014). As reported, due to potentially adverse climate change, since 1950s, agricultural drought-inducible disaster area also had an increasing trend in China—the drought-induced grain loss reached approximate 25–30 billion kg, accounting for 60% of total loss of natural disasters (Jiao et al., 2014; Zhou, 2014). It has been notable that China's agricultural drought becomes more serious mainly due to the adverse climate change and rapid social-economic development.

Maize is one of the most important three staple crops—maize, wheat, and rice, the main resources of the feed, industrial raw materials (Campos et al., 2004; Long et al., 2006; Ribaut et al., 2009), recent years it has ranked first place among the three staple crops (FAO, 2017). In China, it also plays a critical role in food security and husbandry industry development among agricultural and even entire economic sectors at both regional and national levels (Meng et al., 2013; Ma and Ma, 2017; PINC, 2017). Drought is one of major limitations to maize production (Boyer, 1982; Sharp et al., 2004; Xu et al., 2008; Lobell et al., 2014; Avramova et al., 2015), resulting in a yield reduction of 25–30%, even with no harvest in those years of extremely severe drought (Campos et al., 2004; Zhang et al., 2011). In the major maize production zone of USA, the drought sensitivity in maize production in

* Corresponding authors at: State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China.
E-mail addresses: xuzz@ibcas.ac.cn (Z. Xu), gszhou@ibcas.ac.cn (G. Zhou).

https://doi.org/10.1016/j.agrformet.2017.11.023
Received 25 September 2017; Received in revised form 7 November 2017; Accepted 19 November 2017
Available online 25 November 2017
0168-1923/ © 2017 Elsevier B.V. All rights reserved.

recent two decades has been also reported to increase, despite cultivar improvements and the agronomic practices with higher sowing densities (Lobell et al., 2014). Climatic warming is projected to further exaggerate drought's negative impact, leading to huge loss of maize production (Ribaut et al., 2009; Lobell et al., 2014). Drought stress leads to reductions in maize (*Zea mays* L.) and other crops' yields mainly by (i) reducing plant growth and reproductive activities, (ii) reducing photosynthetic potentials and thereby radiation use efficiency (RUE), and (iii) reducing harvest index (HI) (Saini and Westgate, 1999; Earl and Davis, 2003; Barnabás et al., 2008; Xu et al., 2008). Contrastingly, if a maize cultivar root system and its ear growth are not completely limited, and leaf survival is enhanced despite water deficit, the cultivar may be recognized as high drought-tolerant one (Ribaut et al., 2009). Nevertheless, the intermittent drought imposition, and then following rewatering effects on crop plants grown in field still receive a relatively scant attention.

Based on cyclic drought experiment using *Catalpa bungei* species, the accumulative functional effects of progressive drought and subsequent re-watering on plant growth, leaf and root parameters have been found as a useful adaptive mechanism to successive drought and subsequent rewatering (Zheng et al., 2017). As recently reported by Abid et al. (2016), the adaptability to drought, and recovery rate and capacity were closely associated with wheat cultivars. The accumulation of effective metabolites such as sugars, and some amino acids like proline and leucine may exert an adaptive mechanism in response to the drought cyclic patterns (Meyer et al., 2014; Sun et al., 2016; Zheng et al., 2017). In plants of *Lupinus albus*, the new leaves can be produced more as quickly re-watered, although restoration of other metabolites (e.g. sugar content) was lagged (Pinheriro et al., 2004). Maize leaf length undergone one or several days of drought can restore completely following rewatering, but its growth rate could not reach the control level, suggesting that the growth resumption may be only a postponed event, no overcompensation occurrence (Acevedo et al., 1971). It is implied that the magnitude and rate of resumption might depend on pre-drought intensity and its duration (Hsiao, 1973; Xu and Zhou, 2007; Xu et al., 2009, 2010). Thus, the extent of compensation for the limitation of pre-drought by promoting plant growth as rewatering might determine the final plant biomass or crop yield, which may link to drought severity and its duration. Nevertheless, whether plant growth and physiological activities completely recover following rewatering, what are the rate and degree of recovery, and the ability of the adaption to the drying-rewetting cycles might strongly depend on previous drought strength and persistent duration, species and genetic types, and drying-rewetting cycle patterns, which the underlying mechanism is elusive so far (Loewenstein and Pallardy, 2002; Marron et al., 2003; Flexas et al., 2004; Yahdjian and Sala, 2006; Xu et al., 2009, 2010; Sun et al., 2016; Zheng et al., 2017). Thus, responses of plant growth and leaf functional processes to drought history and subsequent rewatering remain to be clarified further, particularly *in situ* crop field.

As stated above, drought effects on plant/crop growth, photosynthesis, and other crucial eco-physiological process have been investigated extensively (e.g., Ne Smith and Ritchie, 1992; Yordanov et al., 2000; Chaves et al., 2002; Harrison et al., 2014). However, as just recently stated by Abid et al. (2016), "studying plants' capability to adapt and recover from drought stress is essential because of the ever-changing nature of drought events". Herein, the objectives of this present study were to: (1) examine the effects of drought episode and rewatering on photosynthetic capacity and chlorophyll fluorescence; (2) compare the leaf functional responses to drought episode and rewatering at different leaf positions from most bottom to upmost leaves, at various plant growth developments; (3) determine changing patterns in responses to drought episode and recovery after rewatering on photosynthetic capacity and chlorophyll fluorescence with the leaf developments; and (4) elucidate the indices for drought adaptability and recovery ability following a pre-drought episode. Our hypotheses are expected: i) drought-episode-induced negative responses may depend on leaf ages/positions and leaf/plant development; ii) the amelioration of drought-induced negative responses by rewatering in field grown maize plants may mainly result from gas exchange behaviors relative to the chlorophyll fluorescence performances—photosystem II (PSII) photochemical processes; iii) the morphological and physiological functional traits may closely interacted, coordinately representing the adaptive responses to episodic drought and following rewetting.

2. Materials and methods

2.1. Site descriptions

The present two-year field experiment was carried out directly *in situ* at an agricultural ecosystem research station during 2015–2016 (41°49′N, 121°12′E, 27.4 m a.s.l.), Jinzhou Ecology and Agricultural Meteorology Center, Jinzhou, Liaoning, a northeastern Chinese province on the renowned northeastern maize production belt (PINC, 2017). This region is located in the northeast of the Eurasian areas, belongs to the warm temperate semi-humid monsoon climate, and atmospheric circulation mainly composes of westerlies and subtropical systems, with clear four seasons. The mean annual temperature is 7.8–9.0 °C, with the extreme maximum temperature of 41.8 °C and the extreme minimum temperature of −31.3 °C; annual frost-free period is 144–180 days; average annual rainfall is 540–640 mm, with 60%–70% of rainfall concentrated in summer. The soil is the typical brown soil, with a soil pH value of 6.3. The soil bulk density, soil field capacity, and wilting coefficient of the soil moisture were 1.61 g cm^{-3}, 22.3%, and 6.5% (gravimetric), respectively. The organic matter and total nitrogen content is 6.41–9.43 g kg^{-1} and 0.69 g kg^{-1}, respectively. The staple crop in this region is maize (Han et al., 2007).

2.2. Experimental design

This study, a maize water-controlled field experiment, was conducted by using a huge mobile rain-proof shelter during two growth seasons of 2015–2016. The two-year experimental design and its results were similar; thus, here the 2016-year results were mainly reported (for 2015-year experimental design and its results, see the Supporting Information File: Table S1 and S2, and Figs. S1–S3). In the 2016-year experiment, the five irrigation treatments were designed: T_1, T_2, T_3, T_4, and T_5 treatments, which denote Control, withholding water during jointing-tasseling, jointing-anthesis, tasseling-milking, and silking-milking, with 260, 188, 138, 136, and 161 mm irrigation amount in entire developmental stage, respectively (Table 1).

There were three replicates in each treatment and 15 plots in total. Each plot is 5 m long and 3 m wide, surrounded by a cement layer to avoid water permeation. The large mobile water-proof shelter is 4 m in height, which is used for simulating precipitation to avoid the rainfall entrance. Maize used in this experiment was a hybrid cultivar, named as Danyu 405, which has been planted widely in recent years in Northern China. Seeds were sowed with 5.3 plants m^{-2} of planting density on 23 May, and the plants were harvested on 25, September 2016. Controlled release fertilizer (N, P_2O_5, and K_2O accounting for 26%, 12%, 12% of the total mass, respectively), was used with 600 kg hm^{-2}.

2.3. Environmental variables and maize traits measurements

2.3.1. Soil relative water content (SRWC) measurements

We used weighing method to measure the soil relative water content. Methods with soil auger were used to retrieve soil samples (0–50 cm), then put the samples to the aluminum specimen box, and weighed the samples to obtain the wet weight. Later, the samples were dried in an oven at 105 °C until a constant weight, and then the dried soil samples were weighed. There were three replicates in each treatment. The SRWC was calculated by the equation below:

Table 1
Simulated rainfall regimes in the field experiment under a rain-shelter.

Growth stage	Irrigation dates(Month/day)	T_1 Irrigating at every 7-day	T_2 Drought episode (27 days)	T_3 Drought episode (41 days)	T_4 Drought episode (41 days)	T_5 Drought episode (34 days)
		Irrigation amount (mm)				
V3~V13	5/24	8.7	8.7	8.7	8.7	8.7
	5/30	0.8	0.8	0.8	0.8	0.8
	6/8	10	10	10	10	10
	6/15	10	10	10	10	10
	6/22	10	10	10	10	10
	6/29	24	24	24	24	24
V13~VT	7/6	24	0	0	24	24
	7/13	24	0	0	24	24
	7/20	25	0	0	0	25
VT~R4	7/27	25	25	0	0	0
	8/3	25	25	0	0	0
	8/10	25	25	25	0	0
	8/17	25	25	25	0	0
	8/24	24	24	24	24	24
Entire period	Total precipitation	260.5	187.5	137.5	135.5	160.5

Notes: The dates measuring photosynthetic parameters are 1, July (V13, jointing); 14, July (V21); 25, July (VT, tasseling); 31, July (R1, Silking); 7, August (R2, blistering); 14, August (R3, milking); 29, August (R4, dough), respectively. Red parts indicate the drought episodes. Relative soil water moisture (0–50 cm depth) decreased to a severe water deficit stress level of 30–40% at the ends of the drought episodes, meanwhile it maintained a normal level of 70–80% in the control plots or after rewatering. The maize growth stage nomenclature refers to Abendroth et al. (2009), http://lib.dr.iastate.edu/extension_pubs/26. Verified 21 July 2017.

SRWC = (Wet soil weight − Dry soil weight)/Dry soil weight/F.C. × 100%

where F.C. (field capacity) is the soil water content measured 24 h after amply wetting the soil.

2.3.2. Chlorophyll content measurements

The relative chlorophyll contents (i.e., SPAD values) of maize leaves were measured by a SPAD–502 m (Minolta Camera Co. Ltd., Japan). We chose 3–5 plants grown healthily for each treatment, and those on each leaf were measured three times on the leaf middle area to avoid the main vein, and then averaged.

2.3.3. Photosynthetic and chlorophyll fluorescence parameters

When measured the photosynthetic parameters, three-five plants grown healthily were chosen for each treatment, with a CIRAS-2 gas exchange system (PP Systems, Hertfordshire, UK). We measured the upper (i.e., the youngest and expanded leaves, 1–2 leaves from the top of the plants), middle (ear leaf or the leaves above or below ear leaf) and lower positions (relative orderly leaves) of each plant, respectively. Instrumentation system provided the red and blue built-in light source, and light intensity (Photosynthetically active radiation, PAR) was set to 1500 μmol m^{-2} s^{-1}. To ensure ample temperature and humidity conditions, the photosynthetic parameters of the maize leaves were measured at 9:00–11:00. The whole measuring process was used an open gas path, air relative humidity was controlled in 50%–70%, CO_2 concentration was controlled in 380–390 μmol mol^{-1}, and leaf temperature was set up at around 27 °C. The parameters included light-saturated net photosynthetic rate (A_{sat}), transpiration rate (E), stomatal conductance (g_s); and the leaf water use efficiency (WUE) was calculated by the formula: WUE = A_{sat}/E.

The chlorophyll fluorescence parameters were measured by using a chlorophyll fluorescence module integrated with the CIRAS-2 gas exchange system at the same part of the same leaves measured simultaneously for the gas exchange parameters. First, the leaves were lighted at a light intensity of 1500 μmol m^{-2} s^{-1} after 15 min to measure the steady-state fluorescence (F_s), and then gave a strong flash (5100 μmol m^{-2} s^{-1}, with pulse time of 0.3 s) to measure the maximum fluorescence (F_m'); later put the leaves under dark adaptation for 3 s, opened the far red after 5 s to measure the minimum light fluorescence (F_o'). According to the expressions, we calculated chlorophyll fluorescence parameters: maximum quantum yield of PSII photochemistry (F_v'/F_m'), quantum yield of PSII electron transport (Φ_{PSII}), photochemical quenching (q_P), and non-photochemical quenching (NPQ) (Genty et al., 1989; van Kooten and Snel, 1990; Maxwell and Johnson, 2000; Kramer et al., 2004):

$$F_v'/F_m' = (F_m'-F_o')/F_m'$$

$$\Phi_{PSII} = (F_m'-F_s)/F_m'$$

$$q_P = (F_m'-F_s)/(F_m'-F_o')$$

$$NPQ = (F_m-F_m')/F_m'$$

2.3.4. Plant height and leaf area measurements

Plant height and leaf area of maize were measured at different stages, and the measured dates were approximately consistent with those for the measurements of photosynthetic and fluorescence parameters. Maximum length and width were measured for each leaf of a maize plant. A conventional formula of the total leaf area per plant was used (Francis et al., 1969):

$$\text{Total leaf area of an entire plant} = \sum_{i=1}^{n} (L_i \times W_i \times 0.75)$$

where i is the leaf order number of the measured plant, n is total number of the plant, Li is leaf maximum length, and Wi leaf maximum width.

2.3.5. Leaf rolling index, leaf erection index, and leaf drooping angle determinations

The upper leaf actual width (at natural state, Ln), maximum width (at unfolding state, Lw), natural length (Lnl), maximum length (Lsl), basic angle of leaf (the angle between leaf and stem), drooping angle (under the naturally bending down of the leaf, the angle between the lines from the pulvinus to the tip and the stem) were determined. Then, the leaf rolling index (LRI, %), leaf erection index (LEI, %), leaf bend degree (LBD, °) were calculated based on Xiang et al. (2012):

$$\text{LRI} = (\text{Lw} - \text{Ln})/\text{Lw} \times 100$$

$$\text{LEI} = \text{Lnl}/\text{Lsl} \times 100$$

$$\text{LBD} = \text{Drooping angle} - \text{Basic angle}.$$

2.3.6. The plant biomass and grain yield

At the end of grain-filling, the tagged plants for measurements of these traits were retrieved, dried at 80 °C to constant weight in a drying oven, and weighed to obtain the plant root, stem, leaf, and grain biomass.

2.4. Data statistics

The statistical analysis was used with SPSS 20.0 software (SPSS Inc., Chicago, IL). One-way ANOVA with Duncan's multiple comparison was used to test the differences in the plant and leaf functional traits and morphological indicators between watering treatments at a 0.05 significant level. The differences of functional parameters among watering treatments, leaf positions and measurement dates were tested by the three-way ANOVA at the 0.05 significant level. The correlations between leaf functional and morphological traits were analyzed with Pearson method. The comprehensive patterns of the responses of leaf functional and morphological traits to episodic drought and rewatering were further analyzed with principal component analysis (PCA, Jolliffe, 2002).

3. Results

3.1. Photosynthetically physiological responses to drought episode and rewatering

3.1.1. Responses in upper leaves

Photosynthetic physiological parameters were measured during the entire growing season: on 1, July (V13, jointing); 14, July (V21); 25, July (VT, tasseling); 31, July (R1, Silking); 7, August (R2, blistering); 14, August (R3, milking); 29, August (R4, dough), respectively (Table 1). As shown in Fig. 1, the upper leaf net light-saturated photosynthetic rate (A_{sat}) of control treatment (T_1) increased with earlier plant development, reaching the maximum of 45.4 μmol m^{-2} s^{-1} on 31, July, thereafter sharply decreasing until to a lowest point of 14.1 μmol m^{-2} s^{-1} by 68.5% at later grain-filling stage.

For the T_2 treatment (withholding water during jointing – tasseling, 27 days), the episodic drought led to a significant decline of A_{sat} with a low level of 21.7 μmol m^{-2} s^{-1} on 14, July, a 40.3% drop; and further downed to a lower level of 15.6 μmol m^{-2} s^{-1} on 25, July, a 65.6% drop. Upon re-irrigating, it rose up to 24.4 μmol m^{-2} s^{-1} by 56.4% relative to the previous value, but not to reach the level of control treatment at the same stage—a maximum of 45.4 μmol m^{-2} s^{-1} for the control plant. It indicated that a 27-day episodic drought from jointing to tasseling significantly inhibited photosynthetic capacity, just a part of recovery when following rewatering occurred, resulting in limitation to plant growth and development, and final grain yield loss.

Leaf A_{sat} of the T_3 treatment (withholding water during jointing – anthesis, 41 days) always markedly decreased, even it remained a low and stable level as rewatering and during anthesis, thereafter declined rapidly after milking until to a low level of 6.6 μmol m^{-2} s^{-1} at later grain-filling. The rewatering had a relatively-higher stimulation relative to the control only at milking, indicating the mild stimulation appeared (17.0 vs: 15.4 μmol m^{-2} s^{-1}, Fig. 1a).

While leaf A_{sat} of the T_4 treatment (withholding water during tasseling–milking, 41 days) had an increase at earlier withholding water (silking stage), then sharply declined to a low level of 12.0 μmol m^{-2} s^{-1} at blistering, thereafter remaining a lower and stable level until the end of the grain-filling, although this time it seemed to lightly rise relative to T_3 treatment, indicating that a stimulation occurred by the just nearly rewatering. Leaf A_{sat} of the T_5 treatment (withholding water during silking–milking, 34 days), similar to T_4 but with less 7-day drought duration, declined even more sharply. It may indicate that later drought at tasseling may result in more sensitive effect on the gas exchange processes.

Other photosynthetically physiological parameters in the upper leaves showed similar change patterns (Fig. 1b–f): For T_2 and T_3 plants, SPAD, g_s, and E markedly deceased 4 weeks after withholding water. However, Φ_{PSII} and F_v'/F_m' remained stable. Rewatering for T_2 on 27, July, and for T_3 on 10, August, resulted in stimulations in SPAD, g_s, E, Φ_{PSII}, and F_v'/F_m'; However, they still could not fully recover to the normal level. The drought stresses of T_4 and T_5 treatments also led to declines in the gas exchange rates, while the chlorophyll fluorescence parameters remained relatively stable except T_4 treatment decrease during drought episode and thereafter rewatering.

3.1.2. Responses in middle leaves

The changes in photosynthetic capacity of leaves at the plant middle position exhibited a similar change pattern in the upper leaves (Fig. 2): As compared to the upper leaves, however, there were lower levels of A_{sat}, SPAD, g_s, and E during drought episodes, while rewatering following the pre-drying also did not lead to a complete restoration in the gas exchange parameters and SPAD values at later grain-filling stage. The chlorophyll fluorescence parameters still maintained a high level, implying that relatively mature middle leaves may have a drought-resistance in terms of PSII photochemical activities as compared with the younger upper leaves.

3.1.3. Responses in bottom leaves

As measured in bottom leaves, there were greater levels in A_{sat} and SPAD under various water treatments at jointing stage (1, July), declining with plant developing (Fig. 3). Plants at normal irrigation (control treatment) showed higher levels in the gas exchange parameters (A_{sat}, g_s, and E) and SPAD values, while lower levels were found during drought episodes, i.e., under T_3, T_4, and T_5 treatments. Only partial recovery was obtained upon rewatering at end of grain-filling stage in the plants experienced pre-drying history (T_4 and T_5 treatments). The chlorophyll fluorescence parameters such as Φ_{PSII} and $F_{v'}/F_{m'}$ were maintained at a higher level as the plants were subjected to withholding water treatments, particularly under T_3 treatment. This again implicates an adaptive response to drought episode in terms of chlorophyll PSII photochemical activities.

The three-way ANOVA showed that watering treatment, leaf position, and measured date produced significant effects on SPAD, A_{sat}, E and WUE, individually ($P < 0.001$; Table 2). Only date as a single factor and the interaction between leaf position and date had significant effects on g_s ($P < 0.05$). The interactions between watering and date, and between leaf position and date significantly affected SPAD, A_{sat}, and E ($P < 0.001$). Effects of leaf position and date alone, and their

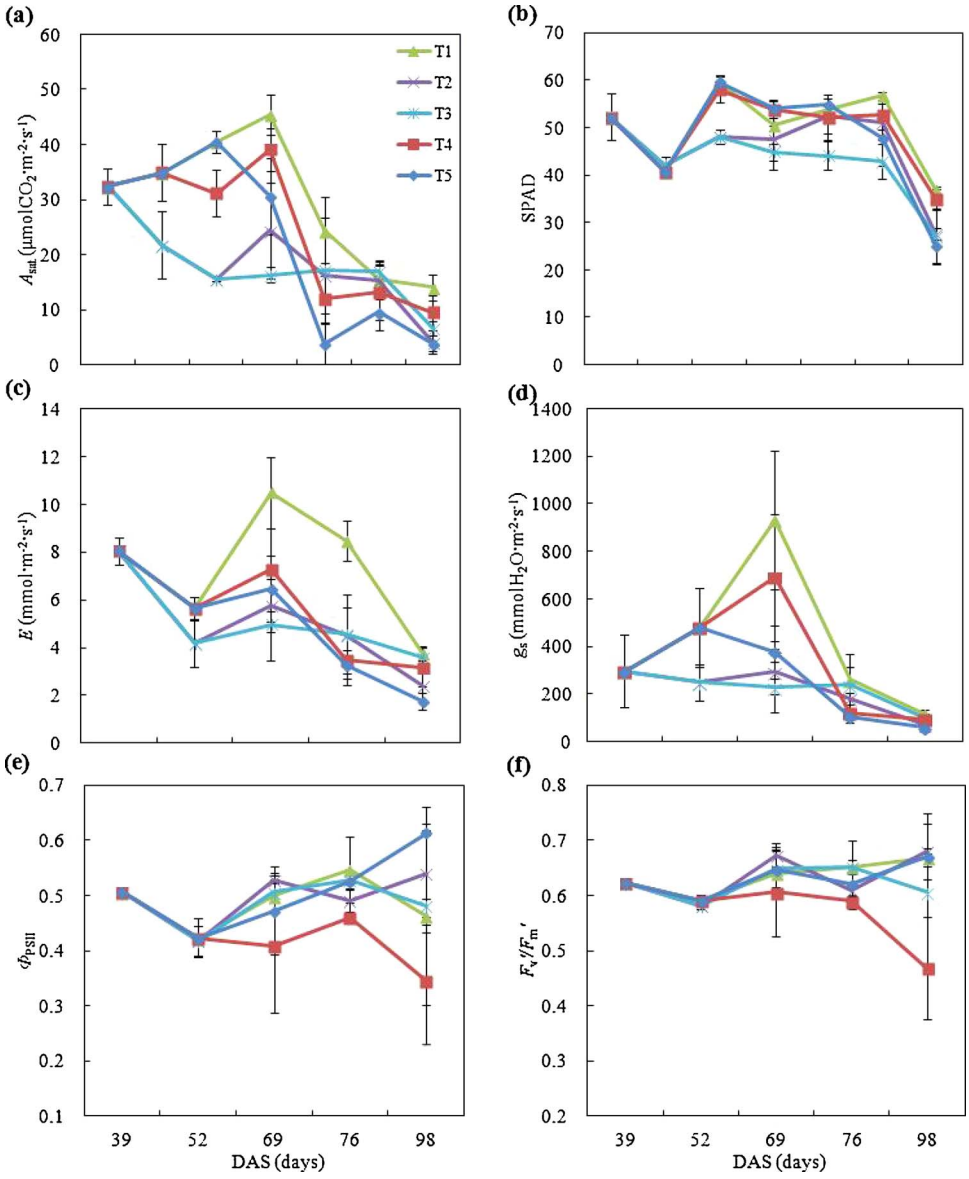

Fig. 1. Effects of drought episode and rewatering on photosynthetic physiological processes in upper leaves.
Notes: DAS, days after sowing; A_{sat}, light-saturated photosynthetic rate; SPAD, relative chlorophyll contents; g_s, stomatal conductance; E, transpiration rate; Φ_{PSII}, PSII actual quantum yield; F_v'/F_m', maximum quantum yield. T_1, T_2, T_3, T_4, and T_5 denote Control, withholding water during jointing-tasseling, jointing-anthesis, tasseling-milking, and silking-milking, with 260, 188, 138, 136, and 161 mm irrigation amount in entire plant development, respectively.

interaction on Φ_{PSII} were significant; while the significant effect on F_v'/F_m' from date as a single factor, and its interaction with leaf position appeared. The interaction of the three factors was not observed ($P > 0.05$).

The 2015-year experiment obtained the similar results on the responses of the relative chlorophyll content (SPAD values) and photosynthetic potentials mainly indicated by fluorescence parameters to the drought episode and the following rewatering regimes at the same experimental site (see Figs. S1–S3).

3.2. Photosynthetically physiological responses in the tagged leaves at different developments

We measured the same leaves tagged to examine the photosynthetically physiological processes at different plant developments/leaf ages and the responses to episodic drought and rewatering—just staring from emerging of the leaves to becoming fully senesced. As showed in Fig. 4, the leaf A_{sat} increased from the initial stage on first July, reaching a maximum on 25 July; thereafter, linearly declining with plant developing or leaf aging (Fig. 4a). A gradual increase in SPAD values was observed initially with a maximum occurrence on 31 July, and a marked decline at end of grain-filling, i.e., 29 August (Fig. 4b). Acute declines in E and g_s were obtained after 31 July (Fig. 4c,d); whereas the two chlorophyll fluorescence parameters (Φ_{PSII} and F_v'/F_m') did not fluctuate greatly (Fig. 4e,f).

As compared to the normal water supply, drought episodes of T_3, T_4, and T_5 treatments resulted in the declines in the tagged leaves' gas exchange parameters—A_{sat}, g_s, and E, particularly with a longer drought persistence; while parts of stimulations by rewatering occurred after an episodic drought (Fig. 4a,c,d). Decreases in SPAD values were often found as the drying episode occurred, particularly at the end of grain-filling (Fig. 4b). We found that the two chlorophyll fluorescence parameters (Φ_{PSII} and F_v'/F_m') had a slight response to either drought episodes or following rewatering, even with relative high levels upon the following rewatering (Fig. 4e,f). This indicated that, in terms of chlorophyll fluorescence parameters, drought-tolerance may be enhanced with the leaf developing or its aging, this issue may need to be investigated further for different crops and their cultivars.

3.3. Responses of leaf morphological traits to drought and rewatering

Changes in maize plant canopy features (plant height, leaf area), leaf morphologic traits (leaf size, leaf rolling index (LRI), leaf erection index (LEI), leaf bend degree (LBD)) in responses to drought episodes

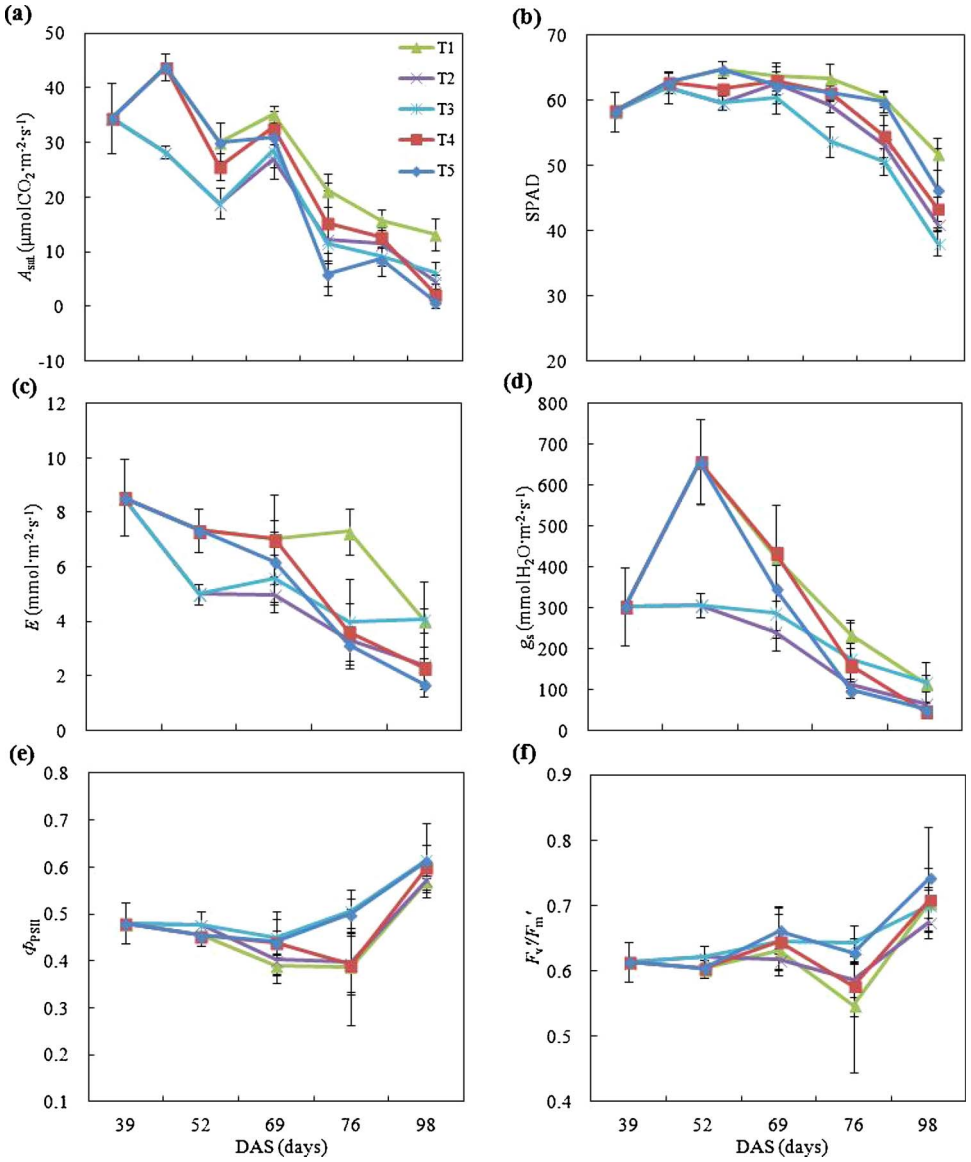

Fig. 2. Effects of drought episode and rewatering on photosynthetic physiological processes in middle leaves.
Notes: DAS, days after sowing; A_{sat}, light-saturated photosynthetic rate; SPAD, relative chlorophyll contents; g_s, stomatal conductance; E, transpiration rate; Φ_{PSII}, PSII actual quantum yield; F_v'/F_m', maximum quantum yield. T1, T2, T3, T4, and T5 denote Control, withholding water during jointing-tasseling, jointing-anthesis, tasseling-milking, and silking-milking, with 260, 188, 138, 136, and 161 mm irrigation amount in entire plant development, respectively

and rewatering were shown in Table 3. The results at first measurement (1, July) showed that no significant changes in plant height, plant individual leaf area, LRI, LEI, and LBD when the plants subjected to the normally watering treatments. LRIs of T_2 and T_3 on 14 July increased significantly due to their undergoing a 15-day drought episode duration. Treatments of T_2 and T_3 reduced plant height and total leaf area, but increased LRI significantly on 25 July, indicating that the two drought treatments significantly affected plant and leaf growth, and morphological traits and canopy structure. LRI of T_3 was greatest under drought on 31 July; and that of T_2 just following rewatering rapidly decreased relative to the previous measurement; and the treatments of T_2 and T_3 had a higher LBD. On 7 August, LRIs under drought conditions, i.e., T_3, T_4 and T_5 treatments, were greater than that of the control, while LEI and LBD were not affected significantly. At milking stage (14 August), LRI under T_4 treatment was greater significantly, and that of T_2 became lower closing to control level due to rewatering. At the end of grain-filling stage (measured on 29 August), T_2 plant leaf area was reduced significantly, whereas LRIs did not differ significantly between the watering treatments. LEIs of T_4 and T_5 treatments were lower, indicating nearly rewatering did not trigger plant leaf erections with leaf aging.

3.4. Relationships between leaf morphological and functional traits in responses to drought and rewatering

Relationships between the morphological and functional traits of upper leaves were given in Table 4. The relationships among SPAD, A_{sat}, E, g_s, and WUE were significant ($P < 0.05$) except the correlations of WUE with E and g_s. There were significant relationships between the two chlorophyll fluorescence parameters—Φ_{PSII} and F_v/F_m themselves; however, they did not correlate with SPAD values, and with gas exchange parameters ($P > 0.05$). Among plant morphological traits, there were significant and positive associations of plant height with total individual plant leaf area, LBD; but negative with LEI. LEI was significantly and negatively correlated with LBD. Between plant morphological and functional traits, there were significant and negative correlations of plant height with A_{sat}, g_s, WUE, and also those of LRI with SPAD, A_{sat}, E, g_s and WUE. Significant positive correlations of LEI with A_{sat} and g_s were found, whereas significant negative correlations of LBD with SPAD, A_{sat}, g_s and WUE appeared, implicating the two leaf morphological indicators (i.e., LEI and LBD) may play an antagonistic role in the responses to drought episode and rewatering.

The correlations between SPAD and A_{sat} were analyzed. The results showed that no significant relationship was observed from jointing to

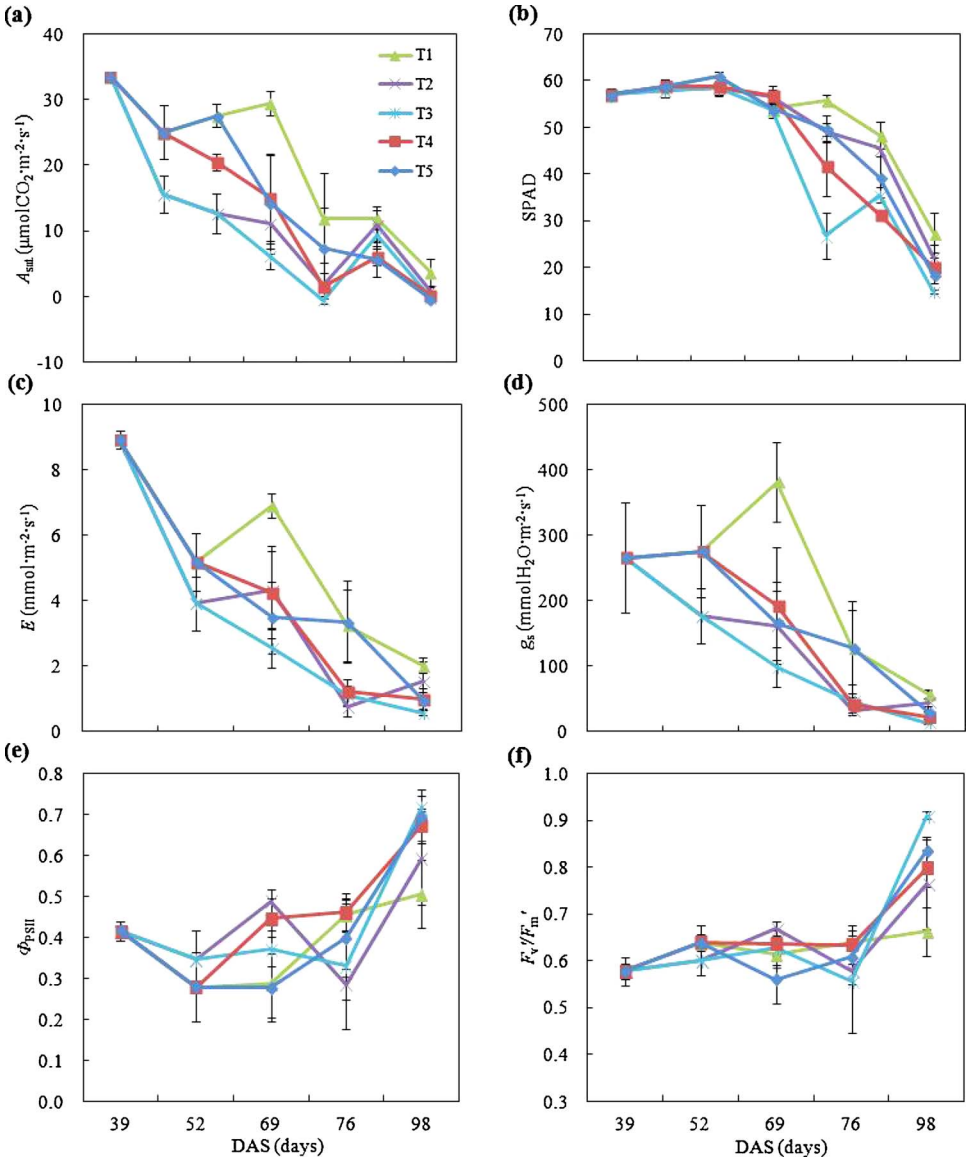

Fig. 3. Effects of drought episode and rewatering on photosynthetic physiological processes in bottom leaves.
Notes: DAS, days after sowing; A_{sat}, light-saturated photosynthetic rate; SPAD, relative chlorophyll contents; g_s, stomatal conductance; E, transpiration rate; Φ_{PSII}, PSII actual quantum yield; F_v'/F_m', maximum quantum yield. T1, T2, T3, T4, and T5 denote Control, withholding water during jointing-tasseling, jointing-anthesis, tasseling-milking, and silking-milking, with 260, 188, 138, 136, and 161 mm irrigation amount in entire plant development, respectively.

tasseling stages (Fig. 5a), whereas significant-positive relationships appeared from silking to blistering ($R^2 = 0.12$, $P < 0.001$), and from milking to denting ($R^2 = 0.41$, $P < 0.001$; Fig. 5b,c), indicating that their correlation becomes stronger with plant developmental process, particularly at later grain-filling. In addition, no significant relationship was found under normal irrigation condition (Fig. 5d), meanwhile the significant relationship appeared under drought episode or rewatering treatments (Fig. 5e,f), implying that their correlation can be enhanced due to the watering treatments.

Based on the principal component analysis (PCA) on leaf functional and morphological traits at silking stage, the first two principal components (PCs) accounted for 60% of the total variations of the maize traits (Fig. 6). Gas exchange parameters closely positively correlated with principle component one (PC1), while the chlorophyll fluorescence parameters closely positively correlated with principle component two (PC2). There were negative correlations of PC2 with SPAD,

Table 2
A significance list based on ANOVA for the effects and their interactions on the traits from watering, leaf position, and date.

	SPAD	A_{sat}	E	g_s	WUE	q_P	NPQ	Φ_{PSII}	F_v'/F_m'
W	< 0.001	< 0.001	< 0.001	0.988	0.007	0.114	< 0.001	0.215	0.946
LP	< 0.001	< 0.001	< 0.001	0.589	< 0.001	< 0.001	0.018	0.005	0.063
Date	< 0.001	< 0.001	< 0.001	0.009	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
W × LP	0.768	0.578	0.469	0.515	0.271	0.825	0.194	0.633	0.399
W × D	< 0.001	0.006	< 0.001	0.324	< 0.001	0.692	< 0.001	0.307	0.512
LP × D	< 0.001	0.002	< 0.001	0.014	0.454	< 0.001	0.178	< 0.001	< 0.001
W × LP × D	0.156ns	0.963ns	0.939ns	0.946 ns	0.452ns	0.692 ns	0.990ns	0.850ns	0.635 ns

Note: P values are given. ns, no significant difference; W, LP, and D denote watering treatment, leaf position, and measurement date, respectively. ×, interaction sign; SPAD, relative chlorophyll content; A_{sat}, light-saturated photosynthetic rate; E, transpiration rate; g_s, stomatal conductance; WUE, water use efficiency; Φ_{PSII}, PSII actual quantum yield; F_v'/F_m', maximum quantum yield; q_P, photochemical quenching; NPQ, non-photochemical quenching.

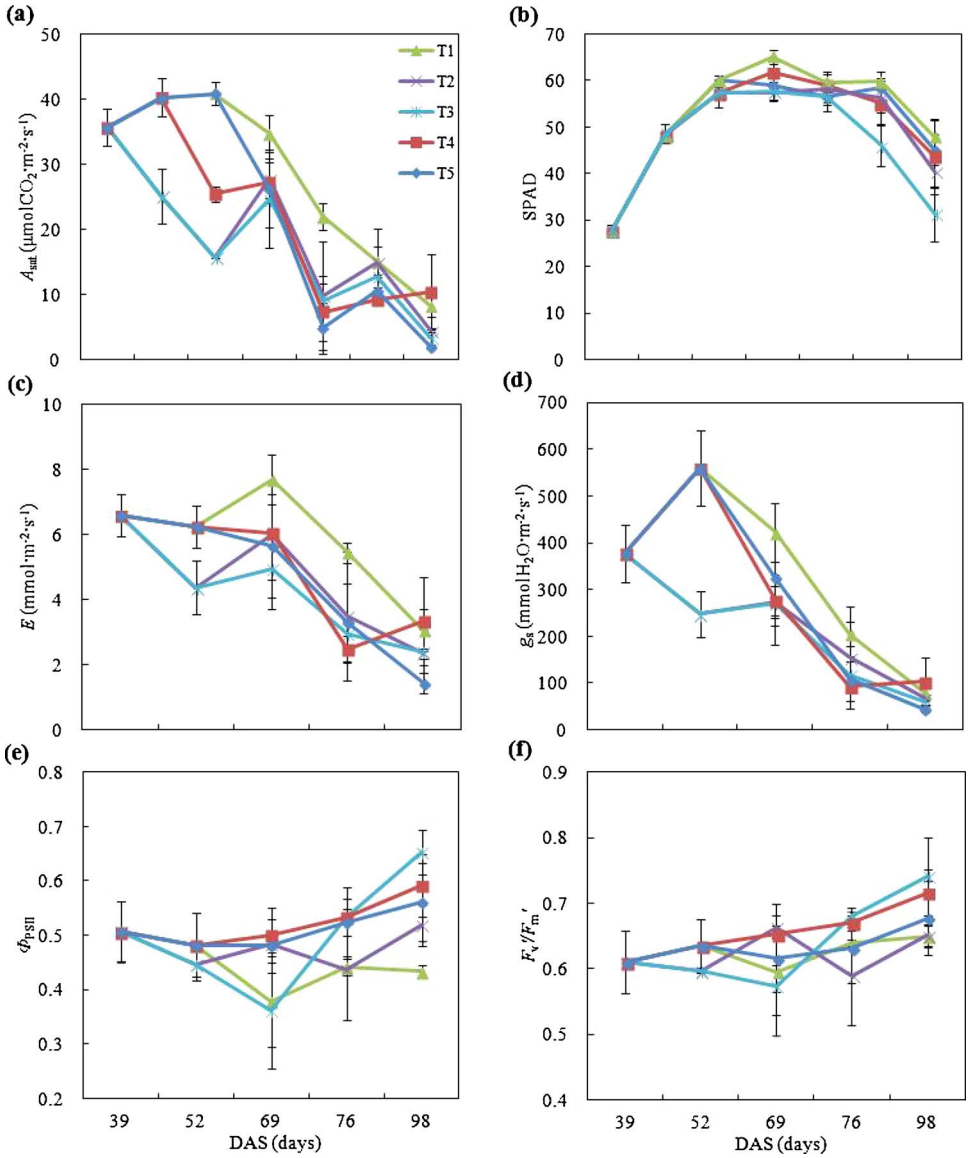

Fig. 4. Photosynthetic physiological changes and the responses to drought episode and rewatering in the tagged leaves.
Notes: DAS, days after sowing; A_{sat}, light-saturated photosynthetic rate; SPAD, relative chlorophyll contents; g_s, stomatal conductance; E, transpiration rate; Φ_{PSII}, PSII actual quantum yield; F_v'/F_m', maximum quantum yield. T_1, T_2, T_3, T_4, and T_5 denote Control, withholding water during jointing-tasseling, jointing-anthesis, tasseling-milking, and silking-milking, with 260, 188, 138, 136, and 161 mm irrigation amount in entire plant development, respectively.

plant height, and leaf area. The loadings were well typically distributed: the gas exchange parameters were located on the right side, the two chlorophyll fluorescence parameters upper part. SPAD was put alone on in quadrant III, while LRI was separated alone in quadrant II. Finally, the two plant growth traits ware located on quadrant IV, contrasting to LRI. Plots of the two factor scores demonstrated that the drought episode treatments (T_4 and T_5) were located on right-bottom parts, which is far from the loadings of gas exchange, chlorophyll fluorescence quantum yields.

4. Discussion

Maize, as one of most important staple crops, playing a critical role in food security and husbandry industry development (Campos et al., 2004; FAO, 2017), is being hampered severely by adverse climate change, such as abnormal precipitation alterations and heat wave events. Drought that is been intensifying by global warming is one of major limitations to maize growth and final grain yield (Boyer, 1982; Sharp et al., 2004; Lobell et al., 2014; Jiao et al., 2014; Avramova et al., 2015; Myers et al., 2017). Although the effect on crop from drought as a single stress factor is studied extensively, understanding the crop functional processes in responses to drought episode and rewatering is still relatively scant, particularly across an entire plant development. The present results indicated that drought during jointing period produced severe effects on vegetative growth and photosynthetic capacity, while continuous drought during tasseling greatly-negatively impacted the reproductive growth and leaf photosynthetic capacity. Rewatering could alleviate adverse effects of pre-drought, but not stimulate both vegetative and reproductive growth and photosynthetic activities to recover fully to the levels of the control. Meanwhile, the leaf chlorophyll fluorescence parameters showed a relatively-stable and adaptive changes in response to episodic drying regimes. Moreover, the leaf functional traits mostly significantly negatively correlated with morphological indicators, and leaf rolling index (LRI) could be a sensitive indicator to assess the response of plants to drought and rewatering. Furthermore, the association of light-saturated net photosynthetic rate (A_{sat}) with chlorophyll content (SPAD value) can be as an effective proxy of leaf aging and the drought episodic durations. The present results may provide a new profound insight into understanding the crops' adaptive mechanism to drought cycle and rewatering regimes, and might be useful for the drought-resistant breeding practices and water-saving irrigation managements.

Nevertheless, the climatic models have well predicted that more extreme climate events will happen by the end of this century, making

Table 3
Effects of drought and rewatering on the plant growth and morphological indicators of maize (2016).

Traits	Treatments	1 Jul	14 Jul	25 Jul	31 Jul	7 Aug	14 Aug	29 Aug
Plant height (m)	T_1	1.434 ± 0.066a	2.014 ± 0.097a	**2.667 ± 0.084a**	2.717 ± 0.119a	**2.734 ± 0.134a**	2.729 ± 0.144a	2.717 ± 0.134a
	T_2	1.336 ± 0.057a	1.897 ± 0.051a	**2.233 ± 0.093b**	2.240 ± 0.084a	**2.232 ± 0.092b**	2.428 ± 0.224a	2.214 ± 0.108a
	T_3	1.476 ± 0.07a	1.897 ± 0.051a	**2.233 ± 0.093b**	2.327 ± 0.132a	**2.436 ± 0.148ab**	2.407 ± 0.157a	2.333 ± 0.199a
	T_4	1.477 ± 0.043a	2.014 ± 0.097a	**2.670 ± 0.045a**	2.710 ± 0.147a	**2.745 ± 0.104a**	2.751 ± 0.110a	2.730 ± 0.099a
	T_5	1.355 ± 0.009a	2.014 ± 0.097a	**2.667 ± 0.084a**	2.463 ± 0.224a	**2.556 ± 0.212ab**	2.527 ± 0.230a	2.520 ± 0.272a
Total leaf area (m^2 $plant^{-1}$)	T_1	0.389 ± 0.025a	0.823 ± 0.035a	**0.998 ± 0.018a**	1.049 ± 0.021a	1.037 ± 0.044a	**0.974 ± 0.017a**	**0.848 ± 0.009a**
	T_2	0.400 ± 0.039a	0.769 ± 0.064a	**0.871 ± 0.034b**	0.890 ± 0.065a	0.930 ± 0.047a	**0.809 ± 0.038b**	**0.643 ± 0.08b**
	T_3	0.437 ± 0.01a	0.769 ± 0.064a	**0.871 ± 0.034b**	0.953 ± 0.097a	0.871 ± 0.054a	**0.686 ± 0.042b**	**0.692 ± 0.082ab**
	T_4	0.423 ± 0.038a	0.823 ± 0.035a	**0.988 ± 0.023a**	1.025 ± 0.002a	0.974 ± 0.016a	**0.768 ± 0.058b**	**0.781 ± 0.012ab**
	T_5	0.363 ± 0.006a	0.823 ± 0.035a	**0.998 ± 0.018a**	0.877 ± 0.078a	0.879 ± 0.067a	**0.837 ± 0.07ab**	**0.738 ± 0.043ab**
Leaf rolling index (LRI, %)	T_1	9.801 ± 0.814a	**13.031 ± 1.87b**	**7.993 ± 2.824b**	**5.381 ± 0.285c**	**9.712 ± 1.127d**	**9.795 ± 1.410c**	12.907 ± 0.682a
	T_2	10.143 ± 0.795a	**19.274 ± 0.614a**	**17.626 ± 1.356a**	**11.702 ± 2.561b**	**12.126 ± 2.358 cd**	**10.453 ± 0.910c**	18.344 ± 4.505a
	T_3	11.116 ± 0.288a	**19.274 ± 0.614a**	**17.626 ± 1.356a**	**23.194 ± 1.653a**	**26.575 ± 0.513a**	**17.24 ± 1.212ab**	18.692 ± 1.192a
	T_4	9.691 ± 1.278a	**13.031 ± 1.87b**	**9.594 ± 1.546b**	**10.163 ± 0.466b**	**16.867 ± 0.658b**	**21.926 ± 2.889a**	18.93 ± 3.082a
	T_5	11.322 ± 1.539a	**13.031 ± 1.87b**	**7.993 ± 2.824b**	**7.336 ± 0.257bc**	**15.059 ± 0.874bc**	**14.641 ± 0.925bc**	12.608 ± 2.55a
Leaf erection index (LEI, %)	T_1	71.734 ± 2.621a	81.218 ± 5.921a	87.103 ± 2.10a	71.813 ± 7.855a	70.960 ± 2.811a	59.500 ± 4.481a	**79.330 ± 7.217a**
	T_2	73.885 ± 0.901a	81.710 ± 6.650a	92.412 ± 1.10a	59.130 ± 6.364a	65.779 ± 1.005a	54.834 ± 5.317a	**65.922 ± 1.196a**
	T_3	70.300 ± 1.434a	81.710 ± 6.650a	92.412 ± 1.10a	56.537 ± 3.256a	61.011 ± 4.763a	50.771 ± 5.036a	**68.788 ± 3.498a**
	T_4	73.822 ± 2.055a	81.218 ± 5.921a	79.918 ± 10.07a	65.282 ± 7.415a	64.864 ± 5.571a	50.230 ± 1.623a	**52.139 ± 3.120b**
	T_5	71.160 ± 6.133a	81.218 ± 5.921a	87.103 ± 2.10a	59.149 ± 8.36a	56.684 ± 7.818a	46.903 ± 3.308a	**49.341 ± 4.209b**
Leaf bend degree (LBD, °)	T_1	37.417 ± 1.856a	16.750 ± 4.116a	9.333 ± 1.764a	**36.222 ± 4.283c**	53.567 ± 6.19a	81.417 ± 9.419a	59.983 ± 20.037a
	T_2	33.000 ± 1.953a	16.000 ± 6.948a	11.783 ± 3.537a	**50.694 ± 5.022ab**	41.833 ± 2.485a	69.167 ± 5.988a	44.233 ± 13.638a
	T_3	39.667 ± 5.516a	16.000 ± 6.948a	11.783 ± 3.537a	**55.833 ± 4.757a**	37.083 ± 7.045a	71.117 ± 7.148a	49.583 ± 18.112a
	T_4	33.917 ± 1.609a	16.750 ± 4.116a	13.833 ± 2.167a	**31.722 ± 3.692c**	45.167 ± 6.749a	65.278 ± 8.084a	83.694 ± 11.916a
	T_5	35.750 ± 3.527a	16.750 ± 4.116a	9.333 ± 1.764a	**37.944 ± 1.811bc**	50.733 ± 2.709a	60.833 ± 6.194a	55.361 ± 4.835a

Note: T_1, T_2, T_3, T_4, and T_5 denote Control, withholding water during jointing-tasseling, jointing-anthesis, tasseling-milking, and silking-milking, with 260, 188, 138, 136, and 161 mm irrigation amount in entire development, respectively. Different little-letters with mean data indicate significant differences between the five watering treatments (bold parts, n = 3–5).

Table 4
Correlation coefficients between the functional and morphological traits of upper leaves.

	SPAD	A_{sat}	E	g_s	WUE	Φ_{PSII}	F_v'/F_m'	Plant height	Plant leaf area	LRI	LEI
A_{sat}	**0.546****										
E	**0.498****	**0.813****									
g_s	**0.427****	**0.845****	**0.816****								
WUE	**0.304***	**0.479****	0.042	0.186							
Φ_{PSII}	−0.152	−0.184	−0.039	−0.143	−0.206						
F_v'/F_m'	−0.111	−0.045	0.045	−0.049	−0.119	**0.911****					
Pant height	−0.232	**−0.391****	−0.168	**−0.316****	**−0.344****	−0.036	−0.02				
Plant leaf area	−0.021	−0.211	−0.035	−0.222	−0.238	−0.015	0.021	**0.854****			
LRI	**−0.436****	**−0.506****	**−0.449****	**−0.422****	−0.204	0.014	−0.039	0.18	0.094		
LEI	0.145	**0.328****	0.217	0.264*	0.227	−0.166	−0.025	−0.298*	−0.185	−0.211	
LBD	**−0.264****	**−0.383****	−0.232	**−0.310***	**−0.279***	0.119	0.007	**0.389****	0.139	0.151	**−0.460****

LRI, leaf rolling index; LEI, leaf erection index; LBD, leaf bend degree. Others see Table 2.
* $P < 0.05$.
** $P < 0.01$ represent significant differences.

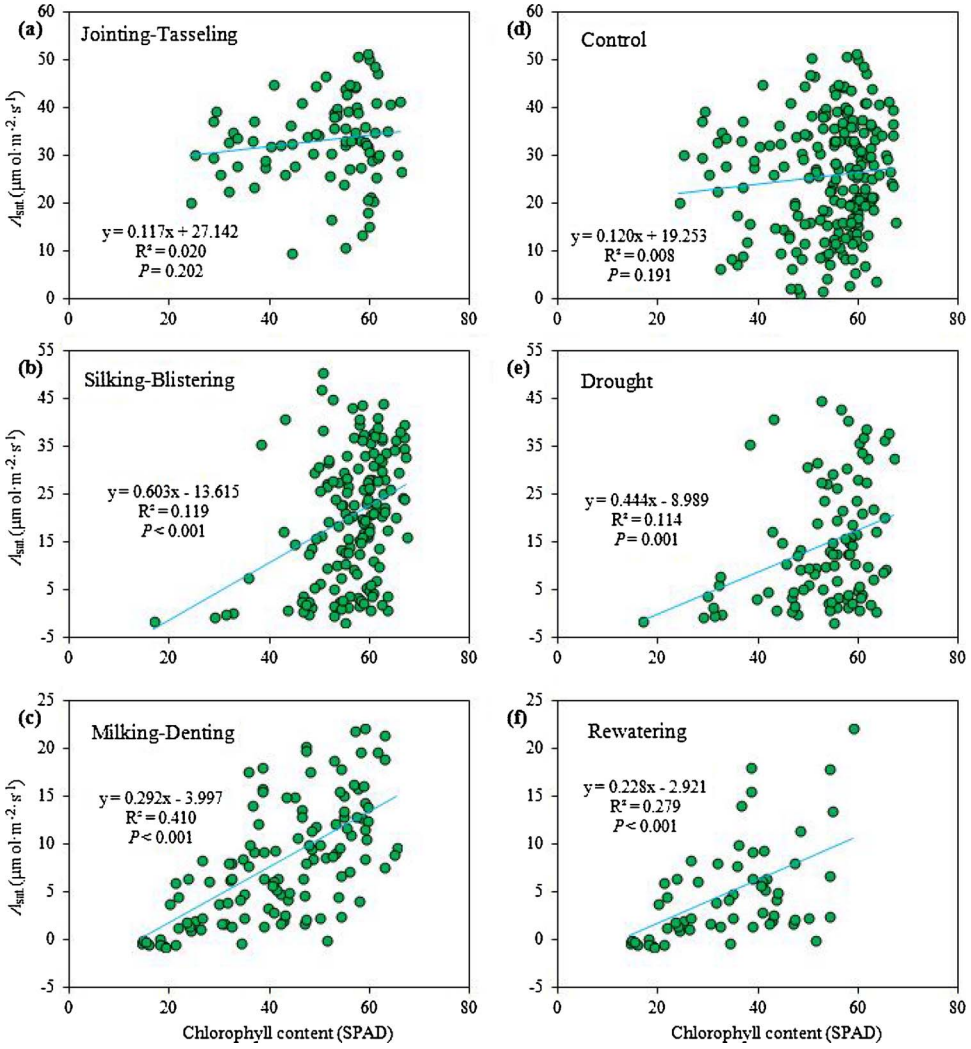

Fig. 5. Effects of drought, rewatering, and plant developmental stages on relationships between light-saturated photosynthetic rate (A_{sat}) and relative chlorophyll content (SPAD readings).

drought severer and heat waves more frequently (Luterbacher et al., 2004; Schär et al., 2004; IPCC, 2014). The consequences of water availability loss have a marked influence on crop growth and productivity (Stuhlfauth et al., 1990; Ciais et al., 2005; Chaves et al., 2009), finally reducing the quantity and quality of grain yield (Marco and Tricoli, 1993; Serraj and Sinclair, 2002; Barnabás et al., 2008; Lobell et al., 2014), and threatening food security regionally even globally (Ghannoum, 2009; Myers et al., 2017). Among them, photosynthesis—the fundamental process for determination of crop growth and its development, even the final grain yield, is primarily affected by crucial climatic change factors such as drought (e.g., Boyer 1982; Chaves, 1991; Jefferies, 1994; Angelopoulos et al., 1996; Farooq et al., 2009; Shen et al., 2015). The current results indicated that changes in the photosynthetically physiological parameters of the upper leaves are most significantly different between the different irrigation treatments ($P < 0.05$). Compared with control, under drought episode, the net light-saturated photosynthetic rate (A_{sat}), chlorophyll content (SPAD value), stomatal conductance (g_s), and transpiration rate (E),

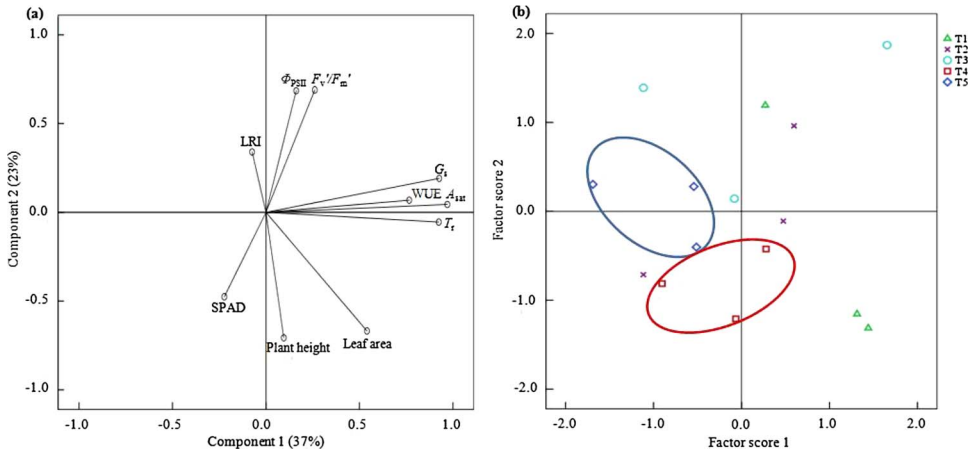

Fig. 6. Principal component analysis on leaf functional and morphological traits and the effects of watering treatments at silking stage.
Notes: LRI, leaf-rolling index; WUE, water use efficiency; red ellipse is for T_4 treatment, while blue one is for T_5 treatment. For others see Fig. 1 and Table 3.

significantly decreased, while the actual quantum efficiency of PSII (Φ_{PSII}), and the effective quantum yield of PSII photochemistry (F_v'/F_m') did no significantly declined. The previous experiments showed that the net photosynthesis rate decreases with g_s dropping (Tenhunen et al., 1987; Jarvis and Davies, 1998; Miyashita et al., 2005). A decrease in g_s will reduce water loss under drought stress, which also generates a drop in CO_2 uptake (Frederick et al., 1989; Miyashita et al., 2005). When the plants of T_2 treatment (pre-anthesis drought episode) was re-watered on 27 July, the photosynthetic parameters of leaves such as A_{sat}, SPAD, g_s, E, Φ_{PSII}, and F_v'/F_m' mostly harmonically increased by the rewatering following the pre-drought episode; the similar responses to rewatering also occurred under T_3, T_4, and T_5 treatments (Figs. 1–3). As reported, precipitation events could generate a rapid response of the plant biological processes, which can trigger plant growth and development (e.g., Acevedo et al., 1971; Reynolds et al., 2004), but the values of photosynthetic parameters generally were lower than control level (Xu et al., 2009; Xu et al., 2010; Suralta et al., 2017). The results illustrated the continuous drought constrained photosynthetic capacity of the upper leaves, and the following rewatering is unable to totally recover to normal level (Figs. 1 and 4). As reported previously, the degree and rate of recovery of rehydration might rely on the duration and severity of pre-drought (Xu and Zhou, 2007; Chen et al., 2009; Xu et al., 2009, 2010; Abid et al., 2016).

The change patterns of middle leaves' photosynthetic parameters were similar to those of the upper leaves (Figs. 1–3): Under the normal treatment, SPAD, A_{sat}, g_s, and E remained at a higher level compared with drought episodes (T_3, T_4, and T_5 treatments). Rewatering did not promote the photosynthetic capacities of T_4 and T_5 at the grain-filling stage. The chlorophyll fluorescence parameters have been ones of the most practical and extensively used indicators to analysis plant eco-physiological processes (e.g., Maxwell and Johnson, 2000). Of them, F_v'/F_m', as most useful one, often ranges between 0.80 and 0.83 without photoinhibition (Björkman and Demmig, 1987). After suffering from severe water deficit stress, F_v'/F_m' would generally decrease (Epron et al., 1992; Souza et al., 2004). However, our results showed both F_v'/F_m' and Φ_{PSII} can maintain a high level even under severe drought particularly in the middle leaves. The results may explain that the middle leaves' period of growth and development is longer, compared with the upper leaves. It may demonstrate a higher drought adaptability in the photochemical process and play a critical role in plant biomass accumulation and final grain yield (also see Allison and Watson, 1966; Xu et al., 2008, 2011; Chen et al., 2016). For the bottom layer leaves, SPAD and A_{sat} were highest at the jointing stage (1 July). Since then, they decreased with plant growing. The influence of drought on the bottom leaves was also consistent with the upper ones. SPAD and gas exchange parameters were also reduced markedly by the drought episode. At the late grain-filling stage (24 August), the stimulating effect of rewatering was also lost partly. The two chlorophyll fluorescence parameters, however, remained higher under and after drought, especially at the end of grain-filling stage (e.g., withholding water from jointing to anthesis stages, total 41-day drought episode). It may again reflect the adaptive ability of maize elder leaves' photochemical activity in responses to drought episodes and thereafter rewetting.

The results of the tagged leaves showed that along with the growth of the same leaf, the changing trends of the photosynthetic physiological parameters under each treatment were various (Fig. 4): under control treatment, A_{sat} remained at a low level measured on 1 July, reaching a maximum on 25 July, thereafter linearly declining. SPAD reached a maximum on 31 July, thereafter significantly decreasing until the late grain-filling stage (29 August). Stomatal conductance and E decreased sharply after 31 July, whereas the changes in chlorophyll fluorescence parameters (Φ_{PSII}, F_v'/F_m') remained stable. The relative chlorophyll content and leaf gas exchange parameters of leaves in normally irrigated plants were at a high level, while those of the plants drought-stricken treatments (T_3, T_4, and T_5 treatments) were at a low level, especially at the later grain-filling stage. It may highlight the leaf senescence process and its enhancement by drought stress (also see Xu et al., 2008, 2010). Rewatering can trigger gas exchange process; the chlorophyll fluorescence parameters (Φ_{PSII}, F_v'/F_m'), however, were less affected by drought stress and rehydration (Lu and Zhang, 1999; but Ghannoum et al., 2003; Gallé et al., 2007). Above all, the results again indicated that the drought-tolerance of the chlorophyll fluorescence parameters may increase with the plant/leaf growth and development when as measured in the same leaves (e.g., the tagged leaves). This issue remains debated, and needs the further research.

With the progresses of the maize plant and leaf growth, the photosynthetic performances of the upper, middle and lower leaves, and the marked leaves of the maize may gradually decrease under moderate and severe drought stresses, and then recover partly after rewatering, which was consistent with previous research results (e.g., Flexas et al., 2009; Vaz et al., 2010; Xu et al., 2011). The current results also found that the photosynthetic performance of the middle leaves was higher than those of the both upper and lower leaves. The reasons may be due to the middle leaves being longer and greater than the upper one, and continuous drought may exacerbate further premature senescence of the bottom leaves (Iacono and Sommer, 2000; Lu et al., 2001; He et al., 2002; Xu et al., 2011). Thus, the middle leaves have stronger photosynthetic performances than both the upper and the lower ones, and they may contribute to most of carbon accumulation as plants exposed to drought episode and the following rewetting.

The sensitivity of crop yield to water deficit often markedly differs at different plant growth stages, which has been a classic study topic (Taylor et al., 1983; Fereres and Soriano, 2007)—Generally, staple crops including maize are more sensitive to water deficit during seedling emergence, flowering, and early grain-filling than those during

early plant growth and late grain-filling periods (e.g., Doorenbos and Kassam, 1979). Under non-lethal water deficit during early vegetative growth, marked reductions in maize plant height and biomass were often found, and its crop phenology could delay, but this may not closely link to a lower yield potential (Damptey and Aspinall, 1976; Abrecht and Carberry, 1993). However, maize plant at jointing stage has exuberantly metabolic activities; thus, if drought occurs from jointing stage to tasseling stage, the inhibition of plant height would be significantly greater than those at other stages (NeSmith and Ritchie, 1992; Earl and Davis, 2003). Therefore, the treatment with withholding water during the jointing period would mainly affect plant vegetative growth, leading to vegetative growth inhibition with short plant size, small leaves and internodes, and delays of tassel and silk emergences, and onset of grain filling, finally a grain yield loss by 15–25% (Damptey and Aspinall, 1976; NeSmith and Ritchie, 1992). The current results indicated that the pre-anthesis drought significantly affected plant height and leaf size, even the canopy structure (and also see Earl and Davis, 2003; Ne Smith and Ritchie, 1992). Çakir (2004) found that the water content in the early growth stage of maize has great influence on plant height, consequently resulting in decline in canopy absorption of PAR (Earl and Davis, 2003). Thus, an early pre-anthesis water deficit might also not be neglected to obtain high yield in maize field, particularly with the severe and consecutive drought events (also see Ne Smith and Ritchie, 1992). Our results manifested that the pre-anthesis drought markedly limited vegetative growth, leading to the declines in plant height and leaf area; and although the rehydration could alleviate the adverse effects from drought, it could not return fully to normal level at either early or later plant development stages. It highlights the drought constraints to maize plant growth during not only drought-persisting but drought-relieving periods. Additionally, leaf rolling index (LRI, Xiang et al., 2012), as a key parameter of plant morphological characteristics, obviously increased during drought episodes, but immediately decreased by rewatering. Therefore, it is suggested that the easy changes in LRI can be as a sensitive indicator for sensing drought and rewatering during almost entire plant growth season.

As stated above, drought stress seriously affected the photosynthesis of maize, inhibited the growth and development, and eventually leading to drops in plant biomass and yield (Irigoyen et al., 1996; Bruce et al., 2002; Zhang et al., 2012). Maize grain yield is highly sensitive to drought during tasseling-silking period, mainly due to the marked decline in grain number (Otegui et al., 1995; Bolanos and Edmeades, 1996; Barnabás et al., 2008). Our results also found that although the plants of T_4 and T_5 treatments were normally irrigated at jointing stage, with the episodic drought at later tasseling stage, the ear growth was still significantly constrained relative to the control group. The current results of T_4 and T_5 treatments (post-anthesis drought) showed no significant effect of drought at tasseling stage on the earlier plant growth. It again highlights that the later drought may exert a greatly adversely influence on the reproductive growth of maize plants.

The analyses on the correlation and principal component analysis (PCA) reveal that there were positive correlations between the functional traits, except those with Φ_{PSII} and F_v'/F_m'; although a positive correlation themselves between Φ_{PSII} and F_v'/F_m' was found. A significant-positive correlation between plant height and total leaf area, and a negative correlation between functional traits and morphological parameters occurred. SPAD is recognized an ideal non-destructive method for testing chlorophyll status in plant leaves, it has been widely used to investigate the environmental adaptability of crops (Manetas et al., 1998; Uddling et al., 2007; Steele et al., 2008; Ciganda et al., 2009; Pour-Aboughadareh et al., 2017). Interestingly, with the development of maize growth, the correlation of A_{sat} and SPAD was more positive and stronger, particularly under drought and rehydration conditions (Fig. 5). Some results showed that the values of SPAD had a higher correlation with actual chlorophyll content under the conditions of lower actual chlorophyll content levels (Steele et al., 2008; Ciganda et al., 2009), depending on species and the chlorophyll distribution on leaf (Uddling et al., 2007). Therefore, probably maize plants grew at later growth stage and moisture condition became stressful, it may lead to reductions in both actual chlorophyll content and photosynthetic performance. Thus, the relationship between A_{sat} and SPAD might become more positive and closer (Fig. 5). It is indicated that the relationships among the functional traits of leaves would alter with plant development and environmental changes, which may become closer and stronger with senescing at the later growth stage and especially under adverse environmental conditions. Additionally, the PCA implicates that the drought episode gave a severe impact on the photosynthetic capacity (Fig. 6), and it may well represent the change patterns in plant and leaf growth, morphological and functional responses to the drought episode and rewatering regimes.

In conclusion, from the current field experiment across two whole plant growth processes, episodic drought may exert markedly negative effects on photosynthetic potentials at either pre-anthesis or post-anthesis stages, particularly during early grain-filling; and the rapid recovery of leaf photosynthetic activities following re-irrigating occurred, but the recovery magnitude and rate might depend on the severity and persistence of the previous drought, and the leaf age and plant development stages. Generally, the leaf gas exchange, and leaf rolling index may demonstrate higher sensitivity to drought episode and thereafter rewatering than these chlorophyll content and its fluorescence parameters. The results would provide a profound insight into how to understand the crop functional traits' responses to various drought stresses and precipitation or irrigation regimes. Finding the appropriate indicators for delayed leaf senescence while increased/stabilized photosynthetic potentials under changing water status may assist us in well dealing with climatic change to ensure crop production stability (Xu et al., 2010; Chen et al., 2013; Ben-Ari et al., 2016). Nevertheless, unambiguous understanding the underlying mechanisms of molecular and eco-physiological responses to various drought events, and helping the staple crops to cope with future climatic change to guarantee food security regionally and globally still remain a huge challenge, which need to be investigated further (Lobell et al., 2014; Gray et al., 2016; Myers et al., 2017).

Acknowledgements

The study was funded by the National Natural Science Foundation of China (41330531), and China Special Fund for Meteorological Research in the Public Interest (GYHY201506019, GYHY201506001-3). The authors are grateful to Na Mi, Fu Cai, Kuiqiao Shi, Yang Yang, Quanhui Ma for their work during the experiment.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2017.11.023.

References

Abendroth, L., Elmore, R., Hartzler, R.G., McGrath, C., Mueller, D.S., Munkvold, G.P., Pope, R., Ric, M.E., Robertson, A.E., Sawyer, J.E., Schaefer, K.J.P., Tollefson, J.J., Tylka, G.L., 2009. Corn Field Guide. Extension and Outreach Publications. Book, pp. 26. Verified 21 July 2017. http://lib.dr.iastate.edu/extension_pubs/26.

Abid, M., Tian, Z., Ata-Ul-Karim, S.T., Wang, F., Liu, Y., Zahoor, R., et al., 2016. Adaptation to and recovery from drought stress at vegetative stages in wheat (*Triticum aestivum*) cultivars. Funct. Plant Biol. 43, 1159–1169.

Abrecht, D.G., Carberry, P.S., 1993. The influence of water deficit prior to tassel initiation on maize growth development and yield. Field Crops Res. 31, 55–69.

Acevedo, E., Hsiao, T.C., Henderson, D.W., 1971. Immediate and subsequent growth responses of maize leaves to changes in water statues. Plant Physiol. 48, 631–636.

Alley, R.B., Marotzke, J., Nordhaus, W.D., Overpeck, J.T., Peteet, D.M., Pielke, R.A., et al., 2003. Abrupt climate change. Science 299, 2005–2010.

Allison, J.C.S., Watson, D.J., 1966. The production and distribution of dry matter in maize after flowering. Ann. Bot. 30, 365–381.

Angelopoulos, K., Dichio, B., Xiloyannis, C., 1996. Inhibition of photosynthesis in olive trees (*Olea europaea* L.) during water stress and rewatering. J. Exp. Bot. 47, 1093–1100.

Avramova, V., AbdElgawad, H., Zhang, Z.F., Fotschki, B., Casadevall, R., Vergauwen, L., Knapen, D., Taleisnik, E., Guisez, Y., Asard, H., Beemster, G.T.S., 2015. Drought induces distinct growth response, protection, and recovery mechanisms in the maize leaf growth zone. Plant Physiol. 169, 1382–1396.
Barnabás, B., Jäger, K., Fehér, A., 2008. The effect of drought and heat stress on reproductive processes in cereals. Plant Cell Environ. 31, 11–38.
Battisti, D.S., Naylor, R.L., 2009. Seeds of doubt response. Science 324 (179-179).
Ben-Ari, T., Adrian, J., Klein, T., Calanca, P., Van der Velde, M., Makowski, D., 2016. Identifying indicators for extreme wheat and maize yield losses. Agric. For. Meteorol. 220, 130–140.
Björkman, O., Demmig, B., 1987. Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. Planta 170, 489–504.
Bolanos, J., Edmeades, G.O., 1996. The importance of the anthesis-silking interval in breeding for drought tolerance in tropical maize. Field Crops Res. 48, 65–80.
Boyer, J.S., 1982. Plant productivity and environment. Science 218, 443–448.
Bruce, W.B., Edmeades, G.O., Barker, T.C., 2002. Molecular and physiological approaches to maize improvement for drought tolerance. J. Exp. Bot. 53, 13–25.
Çakir, R., 2004. Effect of water stress at different development stages on vegetative and reproductive growth of corn. Field Crops Res. 89, 1–16.
Campos, H., Cooper, A., Habben, J.E., Edmeades, G.O., Schussler, J.R., 2004. Improving drought tolerance in maize: a view from industry. Field Crops Res. 90, 19–34.
Chaves, M.M., Pereira, J.S., Maroco, J., Rodrigues, M.L., Ricardo, C.P.P., Osório, M.L., Pinheiro, C., 2002. How plants cope with water stress in the field. Photosynthesis and growth. Ann. Bot. 89, 907–916.
Chaves, M.M., Flexas, J., Pinheiro, C., 2009. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Ann. Bot. 103, 551–560.
Chaves, M.M., 1991. Effects of water deficits on carbon assimilation. J. Exp. Bot. 42, 1–16.
Chen, S., Lin, G., Huang, J., Jenerette, G.D., 2009. Dependence of carbon sequestration on the differential responses of ecosystem photosynthesis and respiration to rain pulses in a semiarid steppe. Glob. Change Biol. 15, 2450–2461.
Chen, X., Chen, F., Chen, Y., Gao, Q., Yang, X., Yuan, L., et al., 2013. Modern maize hybrids in Northeast China exhibit increased yield potential and resource use efficiency despite adverse climate change. Glob. Change Biol. 19, 923–936.
Chen, Y., Wu, D., Mu, X., Xiao, C., Chen, F., Yuan, L., Mi, G., 2016. Vertical distribution of photosynthetic nitrogen use efficiency and its response to nitrogen in field-grown maize. Crop Sci. 56, 397–407.
Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., et al., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437, 529–533.
Ciganda, V., Gitelson, A., Schepers, J., 2009. Non-destructive determination of maize leaf and canopy chlorophyll content. J. Plant Physiol. 166, 157–167.
Damptey, H.B., Aspinall, D., 1976. Water deficit and inflorescence development in *Zea mays* L. Ann. Bot. 40, 23–35.
Doorenbos, J., Kassam, A.H., 1979. Yield Response to Water. FAO Irrigation and Drainage, Paper 33. Food and Agriculture Organization, Rome 257p.
Earl, H.J., Davis, R.F., 2003. Effect of drought stress on leaf and whole canopy radiation use efficiency and yield of maize. Agron. J. 95, 688–696.
Epron, D., Dreyer, E., Breda, N., 1992. Photosynthesis of oak trees [*Quercus petraea* (Matt.) Liebl.] during drought under field conditions: diurnal course of net CO2 assimilation and photochemical efficiency of photosystem II. Plant Cell Environ. 15, 809–820.
FAO, 2017. FAOSTAT. Verified 21 July 2017. http://www.fao.org/faostat/en/#data.
Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., Basra, S.M.A., 2009. Plant drought stress: effects, mechanisms and management. Sustainable Agriculture. Springer, Netherlands, pp. 153–188.
Fereres, E., Soriano, M.A., 2007. Deficit irrigation for reducing agricultural water use. J. Exp. Bot. 58, 147–159.
Flexas, J., Bota, J., Loreta, F., Cornic, G., Sharkey, T.D., 2004. Diffusive and metabolic limitations to photosynthesis under drought and salinity in C_3 plants. Plant Biol. 6, 1–11.
Flexas, J., Barón, M., Bota, J., Ducruet, J.M., Gallé, A., Galmés, J., et al., 2009. Photosynthesis limitations during water stress acclimation and recovery in the drought-adapted vitis hybrid Richter-110 (V. *berlandieri* × *V. rupestris*). J. Exp. Bot. 60, 2361–2377.
Francis, C.A., Rutger, J.N., Palmer, A.F.E., 1969. A Rapid method for plant leaf area estimation in maize (*Zea mays* L.). Crop Sci. 9, 537–539.
Frederick, J.R., Alm, D.M., Hesketh, J.D., 1989. Leaf photosynthetic rates, stomatal resistances, and internal CO_2 concentrations of soybean cultivars under drought stress. Photosynthetica 23, 575–584.
Gallé, A., Haldimann, P., Feller, U., 2007. Photosynthetic performance and water relations in young pubescent oak (*Quercus pubescens*) trees during drought stress and recovery. New Phytol. 174, 799–810.
Genty, B., Briantais, J.-M., Baker, N.R., 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim. Biophys. Acta 990, 87–92.
Ghannoum, O., Conroy, J.P., Driscoll, S.P., Paul, M.J., Foyer, C.H., Lawlor, D.W., 2003. Nonstomatal limitations are responsible for drought induced photosynthetic inhibition in four C_4 grasses. New Phytol. 159, 599–608.
Ghannoum, O., 2009. C_4 photosynthesis and water stress. Ann. Bot. 103, 635–644.
Gray, S.B., Dermody, O., Klein, S.P., Locke, A.M., McGrath, J.M., et al., 2016. Intensifying drought eliminates the expected benefits of elevated carbon dioxide for soybean. Nat. Plants 2, 16132. http://dx.doi.org/10.1038/nplants.2016.132.
Han, G.X., Zhou, G.S., Xu, Z.Z., Yang, Y., Liu, J.L., Shi, K.Q., 2007. Soil temperature and biotic factors drive the seasonal variation of soil respiration in a maize (*Zea mays* L.) agricultural ecosystem. Plant Soil 291, 15–26.
Harrison, M.T., Tardieu, F., Dong, Z., Messina, C.D., Hammer, G.L., 2014. Characterizing drought stress and trait influence on maize yield under current and future conditions. Glob. Change Biol. 20, 867–878.
He, P., Osaki, M., Takebe, M., Shinano, T., 2002. Changes of photosynthetic characteristics in relation to leaf senescence in two maize hybrids with different senescent appearance. Photosynthetica 40, 547–552.
Hsiao, T.C., 1973. Plant responses to water stress. Annu. Rev. Plant Physiol. 24, 519–570.
IPCC, et al., 2014. Climate change 2014: impacts, adaptation, and vulnerability. part A: global and sectoral aspects. In: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D. (Eds.), Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press Cambridge, United Kingdom and New York, NY, USA.
Iacono, F., Sommer, K.J., 2000. Response of electron transport rate of water stress-affected grapevines: influence of leaf age. VITIS 39, 137–144.
Irigoyen, J.J., Juan, J.P., Sanchez-Diaz, M.A.N., 1996. Drought enhances chilling tolerance in a chilling-sensitive maize (*Zea mays*) variety. New Phytol. 134, 53–59.
Iversen, C., Norby, R., 2014. Terrestrial plant productivity and carbon allocation in a changing climate. In: Freedman, B. (Ed.), Global Environmental Change. Springer, Netherlands, pp. 297–316.
Jarvis, A.J., Davies, W.J., 1998. The coupled response of stomatal conductance to photosynthesis and transpiration. J. Exp. Bot. 49, 399–406.
Jefferies, R.A., 1994. Drought and chlorophyll fluorescence in field-grown potato (*Solanum tuberosum*). Physiol. Plant. 90, 93–97.
Jiao, H.Y., Zhou, G.S., Chen, Z.L., 2014. Blue paper about agricultural issues on climate change. Assessment Report on Effect of Climate Change on China' Agriculture (No.1). Social Science Literature Press., Beijing, pp. 1–6.
Jolliffe, I.T., 2002. Principal Component Analysis. Springer, New York.
Kramer, D.M., Johnson, G., Kiirats, O., Edwards, G.E., 2004. New fluorescence parameters for the determination of QA redox state and excitation energy fluxes. Photosynth. Res. 79, 209–218.
Lobell, D.B., Bänziger, M., Magorokosho, C., Vivek, B., 2011. Nonlinear heat effects on African maize as evidenced by historical yield trials. Nat. Clim. Change 1, 42–45.
Lobell, D.B., Roberts, M.J., Schlenker, W., Braun, N., Little, B.B., Rejesus, R.M., Hammer, G.L., 2014. Greater sensitivity to drought accompanies maize yield increase in the US Midwest. Science 344, 516–519.
Loewenstein, N.J., Pallardy, S.G., 2002. Influence of a drying cycle on post-drought xylem sap abscisic acid and stomatal responses in young temperate deciduous angiosperms. New Phytol. 156, 351–361.
Long, S.P., Zhu, X.-G., Naidu, S.L., Ort, D.R., 2006. Can improvement in photosynthesis increase crop yields? Plant Cell Environ. 29, 315–330.
Lu, C., Zhang, J., 1999. Effects of water stress on photosystem II photochemistry and its thermostability in wheat plants. J. Exp. Bot. 50, 1199–1206.
Lu, C., Lu, Q., Zhang, J., Kuang, T., 2001. Xanthophyll cycle, light energy dissipation and photosystem II down-regulation in senescent leaves of wheat plants grown in the field. Aust. J. Plant Physiol. 28, 1023–1030.
Luterbacher, J., Dietrich, D., Xoplaki, E., Grosjean, M., Wanner, H., 2004. European seasonal and annual temperature variability, trends, and extremes since 1500. Science 303, 1499–1503.
Ma, X., Ma, Y., 2017. The spatiotemporal variation analysis of virtual water for agriculture and livestock husbandry: a study for Jilin province in China. Sci. Total Environ. 586, 1150–1161.
Manetas, Y., Grammatikopoulos, G., Kyparissis, A., 1998. The use of the portable, non-destructive, SPAD-502 (Minolta) chlorophyll meter with leaves of varying trichome density and anthocyanin content. J. Plant Physiol. 153, 513–516.
Marco, G.D., Tricoli, D., 1993. Effect of water deficit on photosynthesis and electron transport in wheat grown in a natural environment. J. Plant Physiol. 142, 156–160.
Marron, N., Dreyer, E., Boudouresque, E., Delay, D., Petit, J.-M., Delmotte, F.M., Brignolas, F., 2003. Impact of successive drought and re-watering cycles on growth and specific leaf area of two *Populus* × *canadensis* (Moench) clones, 'Dorskamp' and 'Luisa Avanzo'. Tree Physiol. 23, 1225–1235.
Maxwell, K., Johnson, G.N., 2000. Chlorophyll fluorescence—a practical guide. J. Exp. Bot. 51, 659–668.
Meng, Q., Hou, P., Wu, L., Chen, X., Cui, Z., Zhang, F., 2013. Understanding production potentials and yield gaps in intensive maize production in China. Field Crops Res. 143, 91–97.
Meyer, E., Aspinwall, M.J., Lowry, D.B., Palacio-Mejía, J.D., Logan, T.L., Fay, P.A., Juenger, T.E., 2014. Integrating transcriptional metabolomic, and physiological responses to drought stress and recovery in switchgrass (*Panicum virgatum* L.). BMC Genom. 15, 527–542.
Miyashita, K., Tanakamaru, S., Maitani, T., Kimura, K., 2005. Recovery responses of photosynthesis, transpiration, and stomatal conductance in kidney bean following drought stress. Environ. Exp. Bot. 53, 205–214.
Myers, S.S., Smith, M.R., Guth, S., Golden, C.D., Vaitla, B., Mueller, N.D., Dangour, A.D., Huybers, P., 2017. Climate change and global food systems: potential impacts on food security and undernutrition. Annu. Rev. Public Health 38, 259–277.
Ne Smith, D.S., Ritchie, J.T., 1992. Short and long term responses of corn to a pre anthesis soil water deficit. Agron. J. 84, 107–113.
Otegui, M.E., Andrade, F.H., Suero, E.E., 1995. Growth water use, and kernel abortion of maize subjected to drought at silking. Field Crops Res. 40, 87–94.
PINC, 2017. Crops Database Planting Information Network of China. Verified, 21 July, 2017. http://zzys.agri.gov.cn/nongqing.aspx.
Pinheriro, C., Passarinho, J.A., Ricardo, C.P., 2004. Effect of drought and rewatering on the metabolism of *Lupinus albus* organs. J. Plant Physiol. 161, 1203–1210.
Pour-Aboughadareh, A., Ahmadi, J., Mehrabi, A.A., Etminan, A., Moghaddam, M., Siddique, K.H., 2017. Physiological responses to drought stress in wild relatives of

wheat: implications for wheat improvement. Acta Physiol. Plant 39, 106. http://dx.doi.org/10.1007/s11738-017-2403-z.
Reynolds, J.F., Kemp, P.R., Ogle, K., Fernández, R.J., 2004. Modifying the ápulse-reserve' paradigm for deserts of north America: precipitation pulses, soil water, and plant responses. Oecologia 141, 194–210.
Ribaut, J.-M., Beran, J., Monneveux, P., Setter, T., 2009. Drought tolerance in maize. In: Bennetzen, J.L., Hake, S.C. (Eds.), Handbook of Maize: Its Biology. Springer Science + Business Media, pp. 311–344.
Rurinda, J., Mapfumo, P., van Wijk, M.T., Mtambanengwe, F., Rufino, M.C., Chikowo, R., Giller, K.E., 2014. Comparative assessment of maize, finger millet and sorghum for household food security in the face of increasing climatic risk. Eur. J. Agron. 55, 29–41.
Saini, H.S., Westgate, M.E., 1999. Reproductive development in grain crops during drought. Adv. Agron. 68, 59–96.
Schär, C., Vidale, P.L., Lüthi, D., Frei, C., Häberli, C., Liniger, M.A., et al., 2004. The role of increasing temperature variability in European summer heatwaves. Nature 427, 332–336.
Serraj, R., Sinclair, T.R., 2002. Osmolyte accumulation: can it really help increase crop yield under drought conditions? Plant Cell Environ. 25, 333–341.
Sharp, R.E., Poroyko, V., Hejlek, L.G., Spollen, W.G., Springer, G.K., Bohnert, H.J., Nguyen, H.T., 2004. Root growth maintenance during water deficits: physiology to functional genomes. J. Exp. Bot. 55, 2343–2351.
Shen, X., Dong, Z., Chen, Y., 2015. Drought and UV-B radiation effect on photosynthesis and antioxidant parameters in soybean and maize. Acta Physiol. Plant. 37, 1–8.
Souza, R.P., Machado, E.C., Silva, J.A.B., Lagôa, A.M.M.A., Silveira, J.A.G., 2004. Photosynthetic gas exchange, chlorophyll fluorescence and some associated metabolic changes in cowpea (*Vigna unguiculata*) during water stress and recovery. Environ. Exp. Bot. 51, 45–56.
Steele, M.R., Gitelson, A.A., Rundquist, D.C., 2008. A comparison of two techniques for nondestructive measurement of chlorophyll content in grapevine leaves. Agron. J. 100, 779–782.
Stuhlfauth, T., Scheuermann, R., Fock, H.P., 1990. Light energy dissipation under water stress conditions contribution of reassimilation and evidence for additional processes. Plant Physiol. 92, 1053–1061.
Sun, C., Gao, X., Chen, X., Fu, J., Zhang, Y., 2016. Metabolic and growth responses of maize to successive drought and re-watering cycles. Agric. Water Manag. 172, 62–73.
Suralta, R.R., Kano-Nakata, M., Niones, J.M., Inukai, Y., Kameoka, E., Tran, T.T., et al., 2017. Root plasticity for maintenance of productivity under abiotic stressed soil environments in rice: progress and prospects. Field Crops Res. http://dx.doi.org/10.1016/j.fcr.2016.06.023.
Taylor, H.M., Jordan, W.R., Sinclair, T.R., 1983. Limitations to Efficient Water Use in Production. WIASA, CSSA, SSSA, Madison.
Tenhunen, J.D., Pearcy, R.W., Lange, O.L., 1987. Diurnal variations in leaf conductance and gas exchange in natural environments. In: ZeigerFarquhar, G.D., Cowan, I.R. (Eds.), Stomatal Function. Stanford University Press, Stanford, California, pp. 323.
Trenberth, K.E., Dai, A., Van Der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R., Sheffield, J., 2014. Global warming and changes in drought. Nat. Clim. Change 4, 17–22.
Uddling, J., Gelang-Alfredsson, J., Piikki, K., Pleijel, H., 2007. Evaluating the relationship between leaf chlorophyll concentration and SPAD-502 chlorophyll meter readings. Photosynth. Res. 91, 37–46.
van Kooten, O., Snel, J.F.H., 1990. The use of chlorophyll fluorescence nomenclature in plant stress physiology. Photosynth. Res 25, 147–150.
Vaz, M., Pereira, J.S., Gazarini, L.C., David, T.S., David, J.S., Rodrigues, A., et al., 2010. Drought-induced photosynthetic inhibition and autumn recovery in two Mediterranean oak species (*Quercus ilex* and *Quercus suber*). Tree Physiol. 30, 946–956.
Xiang, J.J., Zhang, G.H., Qian, Q., Xue, H.W., 2012. Semi-rolled leaf1 encodes a putative glycosylphosphatidylinositol-anchored protein and modulates rice leaf rolling by regulating the formation of bulliform cells. Plant Physiol. 159, 1488–1500.
Xu, Z.Z., Jiang, Y.L., Zhou, G.S., 2016. Nitrogen cycles in terrestrial ecosystems: climate change impacts and mitigation. Environ. Rev. 24, 132–143.
Xu, Z.Z., Zhou, G.S., 2007. Photosynthetic recovery of a perennial grass *Leymus chinensis* after different periods of soil drought. Plant Prod. Sci. 10, 277–285.
Xu, Z.Z., Zhou, G.S., Wang, Y.L., Han, G.X., Li, Y.J., 2008. Changes in chlorophyll fluorescence in maize plants with imposed rapid dehydration at different leaf ages. J. Plant Growth Regul. 27, 83–92.
Xu, Z.Z., Zhou, G.S., Shimizu, H., 2009. Are plant growth and photosynthesis limited by pre-drought following rewatering in grass? J. Exp. Bot. 60, 3737–3749.
Xu, Z.Z., Zhou, G.S., Shimizu, H., 2010. Plant responses to drought and rewatering. Plant Signal. Behav. 5, 649–654.
Xu, Z.Z., Zhou, G.S., Han, G.X., Li, Y.J., 2011. Photosynthetic potential and its association with lipid peroxidation in response to high temperature at different leaf ages in maize. J. Plant Growth Regul. 30, 41–50.
Yahdjian, L., Sala, O.E., 2006. Vegetation structure constrains primary production response to water availability in the Patagonian steppe. Ecology 87, 952-962.
Yordanov, I., Velikova, V., Tsonev, T., 2000. Plant responses to drought, acclimation, and stress tolerance. Photosynthetica 38, 171–186.
Zhang, R.H., Xue, J.Q., Pu, J., Zhao, B., Zhang, X.H., Zheng, Y.J., Bu, L.D., 2011. Effects of drought stress on plant growth and photosynthetic characteristic of maize seedlings. Acta Agron. Sin. 37, 521–528.
Zhang, L., Gao, M., Hu, J., Zhang, X., Wang, K., Ashraf, M., 2012. Modulation role of abscisic acid (ABA) on growth: water relations and glycinebetaine metabolism in two maize (*Zea mays* L.) cultivars under drought stress. Int. J. Mol. Sci. 13, 3189–3202.
Zheng, H., Zhang, X., Ma, W., Song, J., Rahman, S.U., Wang, J., Zhang, Y., 2017. Morphological and physiological responses to cyclic drought in two contrasting genotypes of Catalpa bungei. Environ. Exp. Bot. 138, 77–87.
Zhou, G.S., 2014. Research perspectives on effect of climate change on China' Agricultural production. Meteorol. Environ. Sci. 38, 80–94.